INSTABILITY AND DIURNAL VARIATION IN SIZE OF WINTER GROUPINGS OF FIELD ROE DEER

Carole MARCHAL[1,2], Jean-François GERARD[1], Bernard BOISAUBERT[2] & Eric BIDEAU[1]

INTRODUCTION

The European roe deer (*Capreolus capreolus*) is traditionally considered as a typically forest-dwelling deer, one of the characteristics of which is to live in small groups (Eisenberg, 1981; Bideau *et al.,* 1983; Putman, 1988; Gerard *et al.,* 1995). Nevertheless, for a few tens of years, the roe has colonized open cultivated plains and, in this new environment, has been reported to live in groups much larger than those recorded in forests, especially outside the growing season (i.e. when the fields are really open because of the low height of the crops).

This recent phenomenon has been described by numerous authors (e.g. Kaluzinski, 1974; Zejda, 1978; Stüwe & Hendrichs, 1984; Maublanc *et al.,* 1985; Cibien *et al.,* 1989; Gerard *et al.,* 1995). However, the degree of stability of the groups made up by roe in cultivated plains remains largely unkown. This facet of roe social organization is of importance because, as suggested by recent models (Gerard & Loisel, 1995; Gueron & Levin, 1995; Gerard *et al.,* 1997), group instability may explain (at least in terms of proximate causation) the recorded increase of group size with habitat openness (Gerard *et al.,* 1995). Indeed, group instability implies that, in a given population, mean group size corresponds to a balance between group fragmentation and aggregation. Group fusion, provided it basically relies on attraction between individuals, should further be favoured by any increase of the distance at which animals can perceive one another. So, if roe groupings are unstable, mean group size might have increased when the species colonized open plains simply because the increased possibility of perceiving congeners displaced the balance between group fragmentation and aggregation.

In the present paper, we provide a quantification of the instability of field roe's winter groupings, as well as a description of the immediate causes of this instability. Moreover, we look at whether group size increases between sunrise and sunset, and whether aggregation is more frequent than fragmentation in the hours

[1] Institut de Recherche sur les Grands Mammifères, I.N.R.A., Chemin de Borde Rouge, B.P. 27, F-31326 Castanet-Tolosan Cedex, France.

[2] Office National de la Chasse, C.N.E.R.A. Cervidés-Sanglier, 1 Place Exelmans, F-55000 Bar-le-Duc, France.

following sunrise. This should, indeed, be expected if group instability and the possibility of perceiving congeners largely condition the size of roe winter groupings. The distance at which roe can see one another is undoubtedly shorter at night than during the day. Accordingly, mean group size should be smaller at sunrise (after several hours of reduced visibility) than at sunset. Furthermore, any increase in mean group size implies a decrease in the number of groups (provided population size is fixed). So, if mean group size increases in the hours following sunrise, we could expect, in parallel, predominance of fusion over breakup.

MATERIAL AND METHODS

STUDY AREA

The study was carried out in a 2,415-hectare area, located immediately South of the little town of Marle (49° 44' N, 3° 47' E), in the agricultural region of Picardie, Northern France. The area has a mild and regular climate, with almost no snowfall in winter. Average annual rainfall was 811 mm in 1992-1994. During the same period, minimum and maximum temperatures averaged 0.5 °C and 6.2 °C in February (coldest month), and 13.2 °C and 25.0 °C in July (warmest month).

The study area, 61-137 m above sea level, was very flat in most places. More than 85 % of it was made up of large cultivated fields (20 ha on average). The main crops being wheat, barley, sugar beet and pea (Marchal *et al.,* 1998), most of these fields were ploughed or under winter cereals outside the growing season. Pastures (12 ha total) were scarce, as were hedges (5.4 km total for 142.0 km of field boundaries). The area also included 5 broadleaved woods (176 ha total), the largest of which (142 ha) was located on the western border, in a shallow valley.

The largest carnivore in the area being the red fox (*Vulpes vulpes*), roe other than newly-born fawns had no predators, with the exception of humans. Adult bucks were stalked in July-August, while adults of both sexes were hunted during game drives from October to January.

STUDY POPULATION

The animals of the study population behaved as typical field roe. In winter, they spent most of their time in the fields (89 ± 10 % on average ± SE, for 14 roe radio-tracked in January-February; Marchal, 1998). Furthermore, the winter groups, which reached their maximum size in January-February (1-32 roe per group, with an average of 6.57, isolated deer included) were much larger than those ordinarily recorded in forest (1-8 roe per group, with an average rarely exceeding 2.00; Dzieciolowski, 1979; Bideau *et al.,* 1983; Gerard *et al.,* 1995).

On the basis of the maximum number of deer sighted during a single survey of the area (n = 118), minimum population density was estimated at ca. 5 roe per 100 ha. Using the sex-ratios observed during the surveys performed from November 1993 to January 1994, point estimation of sex-ratio ± SE was 1.05 ± 0.13 males for 1 female in animals < 1 year old, but 0.69 ± 0.05 males for 1 female in animals ≥ 1 year of age. Males exhibit a naturally lower survival rate than females in adult roe deer (Gaillard *et al.,* 1993), but in the present case, the lower proportion of adult males was also due to sex-biased hunting.

The study was conducted from November 1992 to April 1993, and from November 1993 to April 1994. Generally speaking, observations were made using 7×42 binoculars and a 20-40 power scope. Roe were considered as belonging to the same group when they were < 50 m apart and showed similar activities and body orientations (Bideau *et al.,* 1983). Sexes were distinguished on the basis of the presence or absence of antlers and of the shape of the rump patch. Between November and January, animals < 1 year old were distinguished from the animals ≥ 1 year old on the basis of body size, and antler size for males.

Data concerning the dynamics of group fragmentation and aggregation were collected all day long from 3 fixed viewpoints, each affording a large panorama. When several groups were in view at the beginning of an observation session, one of them was chosen on the basis of its proximity and/or because it included tagged deer (see Marchal, 1998). Once its size and composition in age-sex classes had been described, the group was followed as long as possible to record every break up or fusion with another group, as well as the time at which, and the context in which, these events occurred (interaction between deer, human disturbance, etc.). In the event of fragmentation, we noted the size and composition of the resulting groups, as well as the age-sex class of the leaders, if any, at the time of the break up. On aggregation, we noted the size and composition of the group fusing with the focal group, which of the groups approached the other when only one did so, and also the age-sex class of the leader(s) of the approaching group(s), if any.

Data used to estimate mean group size were collected during ground surveys, performed along a 27.8-km fixed transect providing observation throughout the open habitats of the study area. This non-linear transect, established on the network of roads and tracks, was driven along by car from one to two times per week, alternately during the 3 hours after sunrise and the 3 hours before sunset.

DATA ANALYSIS

Because most data concerning group fusion and breakup were recorded between February and April 1994, we did not search for differences within or between winters. Variations in the relative frequencies of group fragmentation and aggregation between sunrise and sunset were investigated dividing the day into five periods: from 0 to 2 hours after sunrise, from 2 to 3 hours after sunrise, from 3 hours after sunrise to 3 hours before sunset, from 3 to 2 hours before sunset, and from 2 to 0 hours before sunset. Day-length fluctuating between November and April, it should be noted that the central period was not of constant duration.

Because of the rather low size of the samples, group size data collected during the two winters were pooled. Moreover, distributions of roe group sizes being far from normal (Gerard *et al.,* 1995), the diurnal variations in mean group size were investigated using non-parametric methods. Considering months as repetitions, the sign test was first used to compare the average size of the groups sighted in the 3 hours after sunrise and the 3 hours before sunset. In order to investigate the diurnal pattern of group size variation in more detail (and again considering months as repetitions), Friedman's χ_r^2 test and the Tukey-like procedure described by Zar (1984) were then used to compare the average size of the groups recorded from 0 to 2 hours after sunrise, from 2 to 3 hours after sunrise, from 3 to 2 hours before sunset, and from 2 to 0 hours before sunset.

RESULTS

DYNAMICS OF GROUP FRAGMENTATION AND AGGREGATION

Group instability during daylight

The fate of 73 groups initially composed of 1 to 30 roe (average: 8.04) was observed over 3 hours or more. These groups, taken as a whole, appeared largely unstable: half of them (37/73) had already broken up or fused with another group after 2 hours 38 minutes of observation. Figure 1 shows the decrease with time of the number of groups whose composition was unaltered.

Relative frequencies of aggregation and fragmentation

Overall, 111 fusions and 84 breakups were recorded during the sessions of group observation. As expected, fusion was more frequent than breakup in the 2 hours following sunrise (70.0 % versus 30.0 %, n = 50; χ^2 = 8.00, df = 1, P < 0.005). Furthermore, as shown in figure 2, fragmentation increased in frequency throughout the daytime, and, in the 2 hours before sunset, it even tended to become slightly predominant (56.9 % versus 43.1 % of fusions, n = 51; χ^2 = 0.96, df = 1, P = 0.327).

Causes of aggregation

Most of the aggregations recorded (107/111) involved two groups, but some (4/111) involved three. Moreover, among the 103 fusions whose exact context is
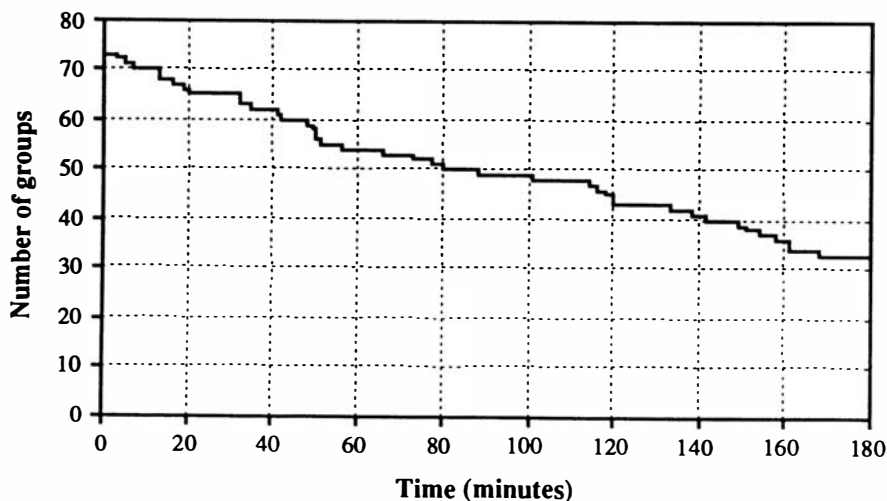

Figure 1. — Decrease with time of the number of roe groups (followed during at least 3 hours) that had not broken up or merged with another group since the beginning of their observation.
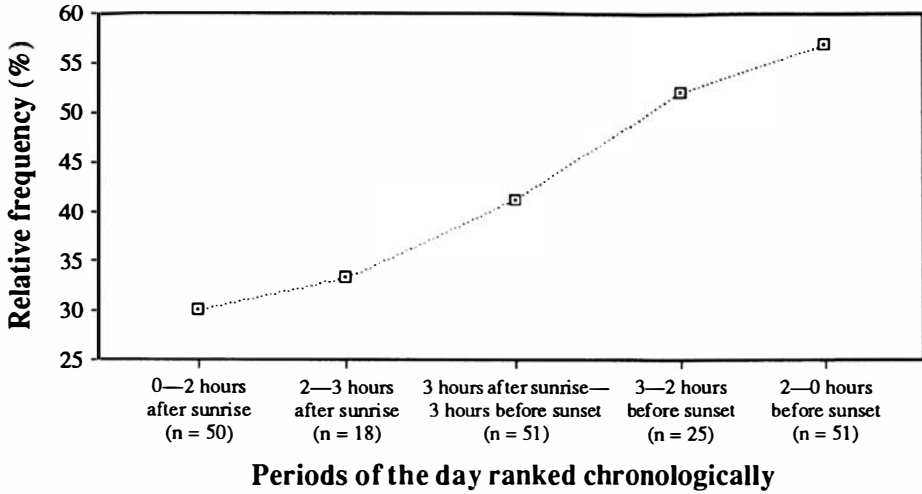
Figure 2. — Relative frequency of breakups (as opposed to fusion) for 5 successive periods of the day, defined by reference to sunrise and sunset (Kendall's correlation coefficient between the relative frequency of breakups and the rank of the day period: $\tau = 1$; $n = 5$; $P < 0.02$).

known, 2.9 % were meetings between individuals which did not seem to have previously perceived each other, 21.4 % were consecutive to a human disturbance, and 75.7 % resulted from a spontaneous attraction between groups whose members indisputably perceived one another. This attraction was almost always asymmetrical since in all cases but one, one group remained at the same place while the other(s) approached. When the groups involved differed in size, the group actively approaching was generally the smaller (76.4 % versus 23.6 %, n = 72; $\chi^2 = 20.06$, df = 1, P < 0.0001). Moreover, 51.2 % of the groups observed approaching (n = 82) had a clear leader, which tended to be slightly more often a female than a male (61.9 % versus 38.1 %; $\chi^2 = 2.38$, df = 1, P = 0.123).

It is worth noting that not all cases of perception between members of distinct groups led to fusion. So, on 22 recorded occasions, the animals of at least one group perceived those of another group but remained at a distance. In 12 other cases, approach occurred but the groups separated after a brief contact.

Causes of fragmentation

Most of the break ups recorded yielded two groups (80/84), but some yielded three (3/84) or even four (1/84). Among the 76 groups for which the context of fragmentation is known, 10.5 % broke up subsequently to human disturbance. Interactions between members of the same group were a rather frequent cause of fragmentation: 7.8 % of the 76 groups observed broke up when a male chased another male away, and 13.2 % split up subsequently to the multiple approach/avoidance behaviour that sometimes occurred in the groups resulting from a recent aggregation. Nevertheless, 68.4 % of the 76 observed fragmentations corresponded to what can be termed "spontaneous departures". In this case, one

individual, alone or followed by others, left the group without any previous visible interactions between group members (on 2 occasions, spontaneous departures occurred simultaneously in more than one direction). In 68.4 % of the cases (n = 57), the group observed leaving had a clear leader, which tended to be slightly more often a female than a male (61.5 % versus 38.5 %; χ^2 = 2.08, df = 1, P = 0.149).

DIURNAL VARIATION IN MEAN GROUP SIZE

Figure 3 shows the monthly variations in the average size of groups sampled throughout the study area in the 3 hours after sunrise and the 3 hours before sunset. As expected, mean group size was higher in the evening than in the morning (unilateral sign test: n + = 6, n – = 0, P < 0.02). Furthermore, when the 3 hours after sunrise and the 3 hours before sunset are each divided into two periods (Table I), Friedman's test confirms that there was an effect of the period of the day on mean group size (χ_r^2 = 12.00; n = 4; k= 6; P < 0.01), and the Tukey-like procedure described by Zar (1984) gives the following result:

early morning < late morning < late evening < early evening

(periods that do not differ significantly at the "experiment-wise error rate" of 0.05 are underscored by the same line). In other words, mean group size increased between early morning and evening. Moreover, it tended to decrease slightly between early and late evening, which is consistent with the pattern of higher group fragmentation over fusion in the late evening.
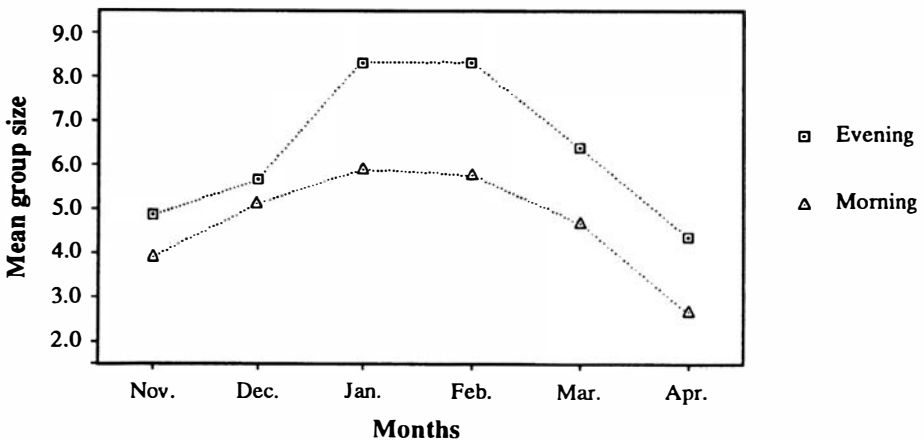

Figure 3. — Monthly variations in the average size of roe groups (solitary animals included) sampled in the 3 hours after sunrise and the 3 hours before sunset.

TABLE I

Monthly variations of the average size of the roe groups (solitary animals included) sampled during four periods of the day.

	November		December		January		February		March		April	
	Mean	n	Mean	n	Mean	n	Mean	n	Mean	n	Mean	n
Early morning	4.10	39	4.77	53	5.71	34	5.38	47	4.26	43	2.44	59
Late morning	3.77	39	5.68	34	6.39	18	6.34	35	5.48	23	3.75	16
Early evening	4.16	19	6.07	41	8.73	22	8.77	13	6.94	32	3.33	3
Late evening	5.38	24	5.10	31	7.25	8	7.83	12	5.52	21	4.83	6

Early morning: from 0 to 2 hours after sunrise; late morning: from 2 to 3 hours after sunrise; early evening: from 3 to 2 hours before sunset; late evening: from 2 to 0 hours before sunset.

DISCUSSION

Our findings are globally consistent with the assumption according to which group instability and the possibility of perceiving congeners at long distances explain the unusually large winter groupings made up by roe in open cultivated plains. Indeed, two prerequisites are satisfied: field roe groupings appear largely unstable, and the attraction between individuals indisputably plays a key role in group fusion. Furthermore, two consequences of the basic assumption are verified: as might be expected on the basis of day/night alternation, mean group size increases between sunrise and sunset, and aggregation is more frequent than fragmentation in the hours following sunrise.

It should be noted, nevertheless, that the roe's activity rhythm might also have some influence on mean group size. Roe typically exhibit two peaks of locomotor/feeding activity, one around sunrise, the other around sunset (Maublanc *et al.,* 1991). Locomotor activity should favour group meeting, but feeding might decrease the attention paid to surrounding congeners. Subsequently, it is not impossible that the equilibrium value towards which mean group size tends is not exactly the same during the peaks of activity and outside them. This might explain why we found a tendency for the mean group size to decrease and fragmentation to become slightly more frequent than aggregation in the two hours before sunset.

The increase of group size in European roe now colonizing open cultivated plains is spectacular because the species is ordinarily known to be a forest-dweller living in small groups. Nevertheless, roe is not the only deer, nor the only wild ruminant in which group size increases with habitat openness. This relationship has, indeed, been found in numerous species of cervids and bovids (e.g. Leuthold, 1970; Peek *et al.,* 1974; Franklin *et al.;* 1975; Hirth, 1977; Evans, 1979; Schaal, 1982; Alados, 1985; Putman, 1988; Barrette, 1991; Estes, 1991). Roe is moreover far from being the only species whose groupings are unstable. Group instability has been reported in many species of wild ruminants (e.g. Feer, 1979; Leuthold, 1979; Murray, 1981; Schaal, 1982; Clutton-Brock *et al.,* 1982; Dubost, 1983; Lott & Minta, 1983; Fichter, 1987; Barrette, 1991; Le Pendu *et al.,* 1995; Mechkour *et al.,* 1997). Accordingly, as already pointed out elsewhere (Gerard & Loisel, 1995;

Gerard *et al.,* 1995), group instability might be suspected to underly the increase of group size with habitat openness in most wild ruminants. In this respect, it would be interesting to determine whether mean group size increases between sunrise and sunset and whether there is a predominance of aggregation over fragmentation after sunrise in species other than the roe deer.

ACKNOWLEDGEMENTS

SUMMARY

The European roe deer (*Capreolus capreolus*) makes up unusually large winter groups in the cultivated plains it has colonized for some decades. In this paper, we investigate the instability of these groups, as well as the possible variations of their average size in the course of the day. The groups observed over at least 3 hours appeared largely unstable: half of them had broken up or fused with another group after 2 hours 38 minutes. Group fusion generally resulted from the spontaneous attraction between groups whose members had perceived one another. Most breakups resulted from the departure of one or more individuals, without any previous visible interactions between group members. Fusion was more frequent than breakups during most of the day. Subsequently, mean group size was larger in the hours before sunset than in the hours following sunrise. The results obtained are globally consistent with the assumption according to which group instability and the increased possibility of perceiving congeners are responsible for the unusually large winter groups made up by roe in cultivated plains.

Key words: social organization, group size, group instability, group dynamics, deer, ungulate, agricultural land, open habitat, colonization.

RÉSUMÉ

Le chevreuil d'Europe (*Capreolus capreolus*) forme en hiver des groupes inhabituellement grands dans les plaines cultivées qu'il colonise depuis quelques décennies. Dans cet article, nous examinons l'instabilité de ces groupes, de même que les éventuelles variations de leur taille moyenne au cours de la journée. Les groupes observés sont apparus nettement instables : la moitié d'entre eux avait éclaté ou fusionné avec un autre groupe après 2 heures 38 minutes d'observation. Les fusions de groupes résultaient en général d'une attraction entre groupes dont

les membres s'étaient indiscutablement perçus. Les éclatements de groupes correspondaient pour la plupart au départ d'un ou plusieurs individus, sans qu'il y ait eu auparavant d'interaction visible entre les membres du groupe. Les fusions étaient plus fréquentes que les éclatements durant la majeure partie de la période diurne. En conséquence, la taille moyenne des groupes était plus grande en fin qu'en début de journée. Les résultats obtenus sont en accord avec l'hypothèse selon laquelle l'instabilité des groupes et la possibilité de percevoir les congénères à grande distance sont à l'origine des grands groupes que le chevreuil a commencé à former lorsqu'il a colonisé les plaines agricoles.

Mots-clés : organisation sociale, taille des groupes, instabilité des groupes, dynamique des groupes, cervidé, ongulé, cultures, milieux ouverts, colonisation.

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